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Increasing aridity affects soil archaeal communities by mediating soil niches in semi-arid regions

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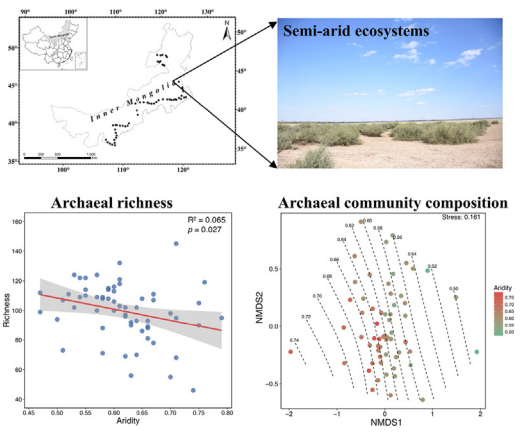
HIGHLIGHTS

- Increasing aridity diminished archaeal richness through improving soil electrical conductivity.
- Different archaeal taxa were present with different levels of aridity.
- Archaeal communities were mainly governed by niche-based processes along the aridity gradient.
- Increasing aridity altered archaeal community composition by changing soil total nitrogen.

GRAPHICAL ABSTRACT



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ABSTRACT

Soil archaea plays a vital role in the functioning of dryland ecosystems, which are expected to expand and get drier in the future as a result of climate change. However, compared with bacteria and fungi, the impacts of increasing aridity on archaea in these ecosystems remain largely unknown. Here, soil samples were collected along a typical aridity gradient in semi-arid regions in Inner Mongolia, China, to investigate whether and how the increasing aridity affects archaeal communities. The results showed that archaeal richness linearly decreased with increasing aridity. After partialling out the effects of soil properties based on partial least squares regression, the significant aridity-richness relationship vanished. The composition of archaeal communities was distributed according to the aridity gradient. These variations were largely driven by the changes in the relative abundance of *Thaumarchaeota*, *Euryarchaeota* and unclassified phyla. Niche-based processes were predominant in structuring the observed archaeal aridity-related pattern. The structural equation models further showed that aridity indirectly reduced archaeal richness through improving soil electrical conductivity (EC) and structured community composition by changing soil total nitrogen (TN). These results suggested that soil salinization and N-losses might be important mechanisms underlying the increasing aridity-induced alterations in archaeal communities, and highlighted the importance of soil niches in mediating the indirect impacts of increasing aridity on archaea.

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1. Introduction

Drylands, including arid, semi-arid and dry-subhumid ecosystems, cover approximately 41% of Earth's land surface with over 38% of the global human population inhabited (Reynolds et al., 2007), and are supposed to be the most susceptible ecosystems to climate change (Maestre et al., 2012). As a consequence of climate-change-driven increases in temperature and frequency of drought events (Easterling, 2000), these areas will experience increasing aridity in the future as forecasted by climate models (Collins et al., 2014; IPCC, 2013). Microbial communities play key roles in soil nutrient cycles (Bardgett and van der Putten, 2014) that are tightly linked to many crucial ecosystem functioning based on plant productivity and soil fertility (Delgado-Baquerizo et al., 2014; Lamarque et al., 2011). Assessing their responses to increasing aridity is of particular importance for predicting alterations in ecosystem functioning under future climate scenarios and developing effective management strategies.

It used to be thought that archaea were only present in extreme environments, but growing evidence indicates that archaea are diverse and widespread on Earth (Schleper et al., 2005). Recently, the archaeal tree has been rapidly expanded with the discovery of new archaeal lineages at different taxonomic levels (Adam et al., 2017). Their crucial roles in mediating biogeochemical processes, such as breakdown of organic matter (Yu et al., 2018), sulfate reduction (Sorokin et al., 2017) and ammonia oxidation (Sauder et al., 2017) have also been well recognized in a wide range of ecosystems. Similarly to soil bacteria and fungi, archaea are also significant or even major components of belowground diversity (Chaban et al., 2006; Angel et al., 2010) and they are altogether responsible for nutrient cycles in terrestrial ecosystems (Kirk et al., 2004; Siles and Margesin, 2016). More importantly, archaeal populations such as ammonia-oxidizing archaea (AOA) preserve a high level of activity (Martens-Habbena et al., 2009; Verhamme et al., 2011) and are more responsible for nitrogen cycle in drylands (Adair and Schwartz, 2008; Valentine, 2007).

Despite the significance of soil archaea, previous studies conducted to determine the effects of increasing aridity on soil microbes have largely focused on bacteria and fungi. It is clear that soil bacteria and fungi respond to increasing aridity in terms of diversity, abundance, biomass and community composition (Chen et al., 2015; Fierer et al., 2012; Hu et al., 2014; Wang et al., 2015), and that aridity promotes these shifts by its effects on plant (Chen et al., 2015) or soil properties (Maestre et al., 2015; Yao et al., 2017). Compared to them, variations in soil archaeal communities resulting from increasing aridity have received much less attention. Limited studies reported that aridity was a significant factor influencing archaeal community composition (Angel et al., 2010; Shi et al., 2016; Wang et al., 2015) and taxa abundance such as *Thaumarchaeota*, *Crenarchaeota* (Auguet et al., 2010; Neilson et al., 2017), and *Euryarchaeota* (Auguet et al., 2010). For patterns of archaeal diversity, however, contradictory results have emerged from different works. Wang et al. (2015) reported that archaeal diversity was greatest in the driest regions, while Angel et al. (2010) proposed that archaeal diversity was not constrained by precipitation. These inconsistent results might be derived from molecular technology adopted in their studies either were low-resolution (Angel et al., 2010) or yielded relatively small numbers of reads (Wang et al., 2015). The lack of taxonomic resolution and precision might hamper the ability to disclose the specific taxa contributing to the observed community differentiation (Fortunato et al., 2013). In addition, although it has been broadly recognized that the niche-based processes and neutral processes simultaneously drive the microbial distribution patterns (Dumbrell et al., 2010; Langenheder and Székely, 2011), their relative influences vary across spatial and temporal scales (Stegen et al., 2012). To date, the primary ecological processes that govern the spatial variation in archaeal community composition along a large-scale aridity gradient have not been addressed.

Understanding the impacts of increasing aridity on soil archaea and the mechanisms underlying those impacts will allow us to better predict ecological systematic responses to climate change in a more holistic view of soil microbes. In this study, we examined whether and how increasing aridity affects archaea along a 1500 km aridity gradient in semi-arid regions in Inner Mongolia, China, which is characterized by contrasting aridity from west to east. A total of 60 samples were collected and high-throughput sequencing with focus on archaeal communities was performed to provide a higher resolution analysis. We hypothesized that (1) there would be a significant aridity-related pattern of archaeal diversity and community composition along the aridity gradient, which are mainly caused by the indirect effect of aridity; (2) there would be some specific taxa that are responsible for the increasing aridity-induced alterations in archaeal communities.

2. Materials and methods

2.1. Study area and sample collection

The current study was carried out in the Inner Mongolia in northern China, with an area of 1.18 million km^2 (Bai et al., 2008). This region is characterized by strong climate gradients (Liu et al., 2008) and provides ideal sites to examine how increasing aridity affects soil archaea. Thus, a 1500 km transect was established in this study, covering a longitude from 107.23 to 122.41°E and a latitude from 37.69 to 49.25°N (Fig. S1). The transect experienced semi-arid continental climate with limited precipitation and the aridity index (AI, the ratio of annual precipitation to annual potential evapotranspiration) ranging from 0.21 to 0.53. The sample collection took place from middle September to early October in 2016, and a total of 60 sites were selected through the entire transect (Fig. S1). The latitude and longitude for each site were recorded using a GPS device during the field work. Soil types of the study sites were arid, sandy, and belonged to desert soils (Bai et al., 2008; Wang et al., 2014). The ground surfaces were characterized by sparse shrubs (*Caragana microphylla Lam.*, *Artemisia ordosica* or *Salix psammophila*) and grasses (*Leymus chinensis*). At each site, an 8 m × 8 m large plot representative of the landscape and dominant vegetation was established. In order to facilitate the comparison between sites with different dominant vegetation, five 0.5 m × 0.5 m quadrats were then randomly placed in bare ground areas within each large plot as previously depicted by Bachar et al. (2010). In each quadrat, random soil samples (0–10 cm) were collected after removing litter and then were mixed thoroughly. Five soil subsamples collecting from quadrats in the same plot were pooled together and homogenized to make a composite sample and were passed through a 2 mm mesh for removing gravel and roots in the field. All soil samples were divided into two parts and sealed in sterilized sampling bags. One part was placed on ice, returned to laboratory as soon as possible and stored at −80 °C until DNA extraction. The other part was transported at ambient temperature and was used immediately for soil properties measurements upon arrival.

2.2. DNA extraction, Illumina sequencing and sequence analysis

The Power soil DNA Kit (MO BIO, Carlsbad, CA, USA) was used to extract total microbial DNA from 0.25 g soil per sample following the manufacturer's recommended instructions. The concentration and purity of the extracted DNA was assessed spectrophotometrically (Nanodrop2000, Thermo Scientific, Waltham, USA). The DNA of high quality was used for polymerase chain reaction (PCR) with the archaeal primer sets 524F10extF 5′-GYCAGCCGCCGCGGTAA-3′ and Arch958RmodR 5′-YCCGGCGTTGAVTCCAATT-3′ (Pires et al., 2012). PCR amplification was individually conducted for each DNA sample in 20-μL volumes including 4 μL of 5 × FastPfu Buffer, 2 μL of 2.5 mM deoxynucleoside triphosphate (dNTP) mix, 0.8 μL of each primer (5 μM), 0.4 μL of FastPfu Polymerase (TeansGen), 0.2 μL of bovine serum albumin (BSA), 10 ng of template DNA and double-distilled H_2O. The PCR

conditions were as follows: 95 °C for 3 min, followed by 35 cycles at 95 °C for 30 s, 55 °C for 30 s, 72 °C for 45 s and a final elongation step at 72 °C for 10 min. After checking the success of amplification via 2% agarose gel, PCR products were purified and quantified using AxyPrep DNA Gel Extraction Kit (Axygen Biosciences, Union City, CA, USA) and quantified using QuantiFluor™ -ST (Promega, Madison, WI, USA), respectively. The purified amplicons per sample were used to prepare DNA library and then paired-end sequencing (2 × 250 bp) was performed on the Illumina Miseq sequencing platform (Illumina, San Diego, USA). The raw archaeal sequences in this study were deposited in Sequence Read Archive (SRA) of NCBI database and were available under accession number SRP149056.

The raw sequences with an average quality score < 20 within a 50 bp sliding window were truncated, after which the truncated sequences shorter that 50 bp in length were discarded using Trimmomatic (Bolger et al., 2014). Paired-end sequences were merged with a minimum overlap of 10 bp and a 20% error rate using FLASH (Magoč and Salzberg, 2011). Chimeric sequences were detected and filtered in USEARCH by running the UCHIME algorithm (Edgar et al., 2011). All of the remaining high-quality sequences were clustered into Operational taxonomic units (OTUs) at 97% similarity threshold using the UPARSE algorithm (Edgar, 2013). For each OTU, the most abundant sequence was regarded as its representative sequence. Taxonomic affiliations of representative sequences were then performed using RDP classifier (Wang et al., 2007). The number of sequence reads ranged from 27,901 to 41,554 per sample with an average length of 447 bp. In order to correct the bias caused by different sequencing depths, the sequence data were normalized to 27,901 sequences per sample.

2.3. Soil properties measurements and climate data collection

A range of soil properties that might potentially contribute to patterns of soil archaeal were measured in this study. Before physicochemical analyses all of the soil samples were air-dried at room temperature for 4 weeks, except soil moisture content which was determined gravimetrically by weighing fresh soil samples before and after oven-drying at 105 °C for 24 h. Soil pH was determined using a pH meter in a soil suspension with a soil: water ratio of 1: 2.5 mass/volume. Soil texture was determined using a Mastersizer 2000 (Malvern Instruments, Malvern, England) after removing of organic matter as described by Hu et al. (2014). Soil electrical conductivity (EC) was measured using a conductivity meter (FE30, Mettler Toledo, Switzerland). Total nitrogen (TN) content was determined using a Kjeltec 2200 Auto Distillation Unit (Foss Tecator AB, Sweden). Soil organic carbon (SOC) was quantified using potassium dichromate oxidation titration method (LY/T, 1237-1999). Total phosphorus (TP) was measured by molybdenum blue method using a UV–visible spectrophotometer (UV-2550, Shimadzu, Japan). Mean annual precipitation (MAP) and mean annual temperature (MAT) of each sampling site were obtained from the China Meteorological Data Sharing Service System (https://data.cma.cn/en), based on which annual potential evapotranspiration (PET) and aridity index (AI) was calculated according to Chen et al. (2014). In order to facilitate and simplify the interpretation of results, aridity was defined as 1-AI, as done by Delgado-Baquerizo et al. (2013a).

2.4. Statistical analysis

All statistical analysis was done using program R v 3.1.4 (R Core Team, 2015) unless stated otherwise. To uncover the relationship between aridity and archaeal diversity, linear and curvilinear regressions were modeled using three different functions: linear, quadratic and logarithm in SigmaPlot v 14.0 (Systat Software Inc., Chicago, IL, USA). The best-fitting model in each case was selected by following the small-sample-size-corrected Akaike Information Criterion (AICc). The lower AICc index the better the model. When differences in AICc values of these models were <2, the linear model was selected (Maestre et al., 2012). Normality tests (Shapiro-Wilk) were performed with the data prior to regression analysis. Variables not normally distributed were log-transformed. Partial least square regression (PLSR) was used as described by Yang et al. (2017) to further test increasing aridity influenced archaeal diversity whether directly or indirectly. In this approach, the relationship between residuals of the model fit to archaeal diversity as a function of the most important component of soil properties and the aridity was determined. If aridity indirectly influenced archaeal diversity by mediating soil properties, the association between them would disappear in the PLSR models (Palpurina et al., 2016). Archaeal diversity and all measured environmental variables including aridity and soil properties were standardized prior to modeling (Yang et al., 2017). PLSR models were set up using package PLS (Mevik and Wehrens, 2007).

Non-metric multidimensional scaling (NMDS) analysis was performed to depict variations in soil archaeal community composition along the aridity gradient, stress values of which below 0.2 were considered acceptable (Zhang et al., 2014). The contour lines of aridity were fitted on the NMDS ordination via ordisurf function (Griffiths et al., 2011). Permutational multivariate analysis of variance (PERMANOVA) was applied to test whether the separation of the archaeal community composition visualized in the NMDS plot was statistically significant. Mantel tests with 9999 permutations were conducted to uncover the correlation between the environmental distance matrix, the geographic distance matrix and the archaeal community similarity (1 minus Bray-Curtis index of dissimilarity), respectively. Similarity matrices, NMDS, PERMANOVA and Mantel test were conducted using vegan package (Oksanen et al., 2015). The geographic distance matrix was calculated using Imap package based on latitudinal and longitudinal coordinates of each site. To tease apart the relative contribution of environmental and geographic factors to the observed variations in archaeal communities along the aridity gradient, multiple regression on matrices (MRM) approach was carried out using ecodist package (Goslee and Urban, 2007). The environmental distance matrix was calculated using Euclidean method based on standardized values of both aridity and soil properties.

Indicator species can distinguish one community from another and characterize a given habitat (Fortunato et al., 2013). In order to find out key taxa that could define distinct regions with different levels of aridity, indicator species analysis (Dufrêne and Legendre, 1997) was performed at the OTU level using the package labdsv (Roberts, 2013). Only OTUs with significant ($p < 0.05$) indicator value index (IndVal) > 0.3 were defined as good indicators (Liao et al., 2016).

Structural equation modeling (SEM) was used to understand the direct or indirect interactions among soil properties, archaeal diversity and community composition in response to increasing aridity. Before the SEM process, hypothetical relationships were proposed by assuming that aridity indirectly affects archaeal communities mainly through altering soil properties. To simply the model, only soil water availability (SM), soil nutrients (C/N ratio and TN), soil EC and clay content and interactions among them were included in the model. Based on the aforementioned assumption, prior models were established independently for archaeal richness (Fig. S2) and community composition (Fig. S3). Archaeal community composition was represented by the relative abundance of major phyla in the subsequent SEM analysis as done by Liu et al. (2018) and Yao et al. (2017). Normal distributions of the data were checked via the Shapiro-Wilk test before modeling, and non-normal distributions were log-transformed to improve their normality. The SEM was carried out by using the lavaan package (Rosseel, 2012). Multiple criteria were necessary for the evaluation of overall goodness of fit for SEM. The robustness of the models in this current investigation was evaluated by Chi-square test (χ^2 test; the model fits the data well when $p > 0.05$), the root mean square error of approximation (RMSEA; the model fits the data well when $0 \le RMSEA \le 0.05$ and $0.10 < p \le 1.00$). Because the model included non-normally distributing variables, the Bollen-Stine bootstrap test (Schermelleh-Engel et al., 2003)

was also conducted to further confirmed the fit of the model (the model fits the data well when 0.10 < bootstrap $p \leq 1.00$) as described by Delgado-Baquerizo et al. (2013a).

3. Results

Illumina sequencing of the 60 soil samples yielded a total of 1,674,060 high-quality sequences, which were all assigned to the taxonomic domain Archaea and were clustered into distinct 659 OTUs. Both the Good's coverage scores (in all cases above 99.9%) and the rarefaction curves which reached the plateau phase (Fig. S4) indicated that the soil archaeal community diversity had been well captured at the current sequencing depth in this study.

3.1. Soil archaeal diversity along the aridity gradient

The relationship between aridity and soil archaeal OTU richness was best approximated by a linear model based on differences in AICc (Table S1). Archaeal communities inhabiting in the less dry regions were more diverse than those in the comparatively drier regions, as archaeal richness decreased significantly with increasing aridity (Fig. 1a). PLSR analysis was conducted to partial out the potential effects of soil properties on archaeal richness, after which the significant aridity-richness association vanished (Fig. 1b), suggesting that aridity had indirect impact on archaeal richness. Similarly, archaeal phylogenetic diversity was also significantly and negatively associated with aridity (Fig. S5a) and this relationship became non-significant after controlling for the potential effects of soil properties (Fig. S5b).

3.2. Soil archaeal community composition along the aridity gradient

The archaeal distribution was visualized using NMDS based on Bray-Curtis dissimilarity. Soil archaeal community composition varied along the aridity gradient and was distributed according to the aridity gradient (Fig. 2a). This result was further corroborated by the significant correlation between distance matrices for archaea and aridity (Table S2). According to the NMDS plot, regions that were more dissimilar in aridity harbored more dissimilar soil archaeal communities (Fig. 2a). In this way, archaeal communities separated into two significantly unique groups: less dry regions with aridity ranging from 0.47 to 0.63 and drier regions with relatively higher aridity ranging from 0.63 to 0.79 (PERMANOVA, $p = 0.004$; Fig. 2). Specifically, the most dominant phylum *Thaumarchaeota* was more abundant in the less dry regions with mean relative abundance of 86.00% than this in the drier regions (79.02%; Fig. 2b and Table S3). While the secondary dominant phylum *Euryarchaeota* was less abundant in less dry regions (11.23%) than in drier regions (14.82%; Fig. 2b and Table S3). Interestingly, some phyla, despite their relatively low abundance, such as *Miscellaneous_Euryarchaeotic_Group* (*MEG*), *Woesearchaeota*, *Diapherotrites* and *Crenarchaeota* were present in less dry regions, but were absent in drier regions (Table S3). Conversely, *Marine_Benthic_Group_E* (*MBG-E*) was only present in drier regions (Table S3). In summary, these results indicated that different archaeal taxa were present along the aridity gradient.

Significant reductions in archaeal community similarity with increasing geographic distance, which satisfied distance-decay relationship, were also observed (Fig. 3). MRM model was then used to determine to what extent the observed variations in archaeal community composition could be explained by the combinations of environmental factors and geographic distance, respectively. A total of 21.24% variation in archaeal community could explained by MRM model and environmental factors showed more effective in explaining the variations than geographic distance did (Table 1, partial regression coefficient b = 0.033 and 4.197E−5, respectively, $p < 0.001$).

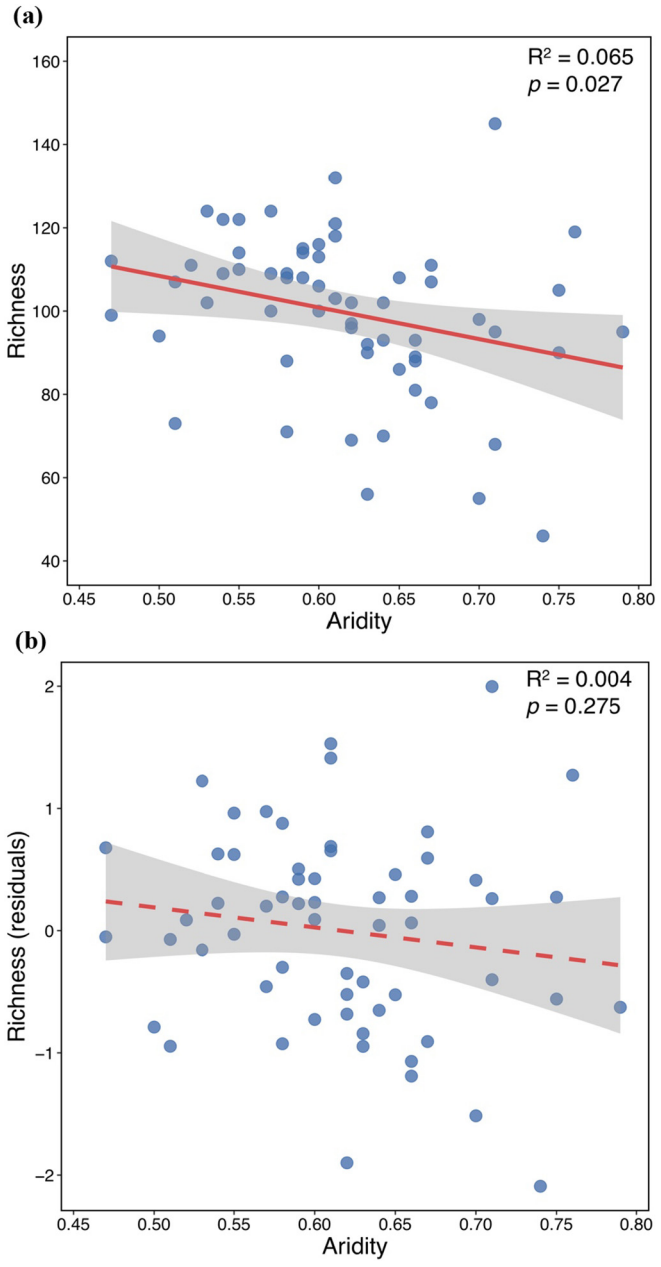

Fig. 1. The relationship between aridity and archaeal richness based on (a) linear regression and (b) partial least square regression (PLSR) that partialed out the confounding effects of all soil properties. Adjusted R^2 with associated *p*-values in each case was shown on the figure. The solid red line represents the significant fitted model ($p < 0.05$), whereas the dashed red line represents the insignificant fitted model. The shaded areas indicate the 95% confidence intervals of the fit.

3.3. The effects of aridity on soil archaeal communities

Structural equation modeling (SEM) was further conducted to provide mechanistic basis for understanding how soil properties mediate alterations in soil archaeal richness and community composition with increasing aridity, respectively. The models all fitted the data well in this study based on the pervious hypothesis (Fig. 4) and they accounted for 27.8% and 89.3% of the variance in archaeal richness and community composition, respectively (Fig. 4). Both soil C/N ratio and soil EC had a negative direct effect on archaeal richness, while soil EC was positively related to aridity among them. Accordingly, increasing aridity had a

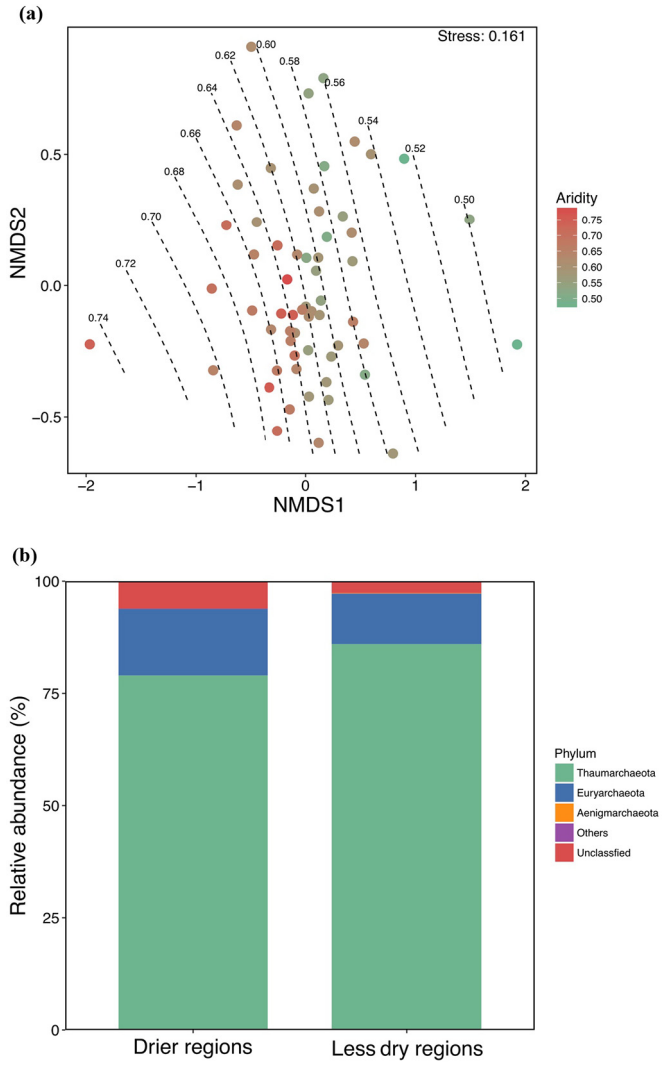

Fig. 2. Variations in soil archaeal community composition along the aridity gradient. (a) Two dimensional NMDS ordination plot of soil archaeal communities based on the Bray-Curtis index of dissimilarity. Samples were color-coded and the color bars represented the aridity. Black dashed lines represented the contour lines of aridity fitted on the NMDS ordination. (b) Taxonomic composition at the phylum level of archaeal communities in soils separated due to aridity categories. Sequences that could not be unambiguously classified at the phylum level were assigned to "Unclassified", known phyla with relative abundance below 0.1% were assigned to "Others".

negative indirect effect on archaeal richness due to increased soil EC (Fig. 4a). With respect to composition, aridity directly and negatively influenced TN, which in turn structured archaeal community composition (Fig. 4b).

3.4. Indicator species differentiated archaeal communities along the aridity gradient

Indicator species analysis was carried out to identify key taxa that distinguished archaeal communities of drier regions to those of less dry regions, based on which a total of 36 OTUs were found significantly associated with aridity (12 OTUs in the direr regions and 24 OTUs in the less dry regions, respectively). A majority of indicator species for less dry regions (70.83%) were affiliated with dominant phyla such as *Thaumarchaeota* and *Euryarchaeota*, whereas 66.67% of indicators for drier regions were unclassified at phylum level (Table S4). All the indictor OTUs for drier regions were significantly and positively related to aridity (Table S4) and were either more abundant or occurred more

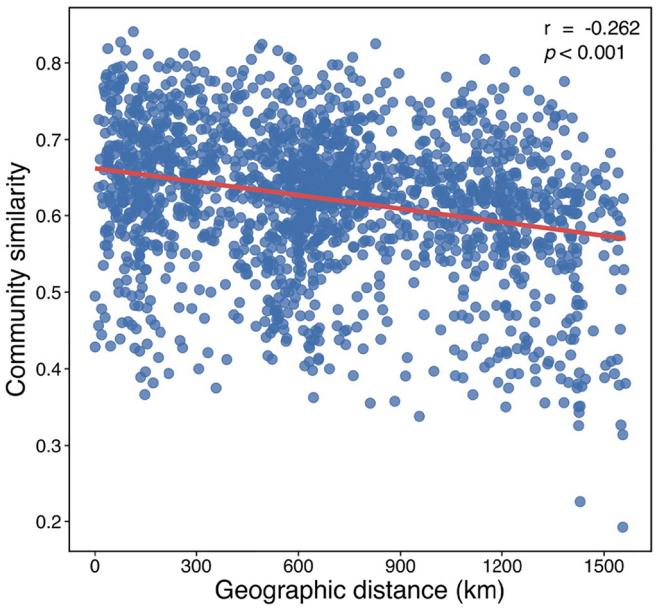

Fig. 3. The distance-decay curve of archaeal community similarity.

frequently than they did in less dry regions (Fig. 5). Likewise, indicator OTUs for less dry regions were characterized by higher relative abundance or higher occurrence compared to that of drier regions (Fig. 5). Among them, OTU432, which showed a significant negative correlation with aridity, was even unique to less dry regions (Fig. 5 and Table S4).

4. Discussion

4.1. Aridity-related patterns of soil archaeal diversity and community composition

In this study, we observed significant reductions in archaeal diversity (richness and phylogenetic diversity) with increasing aridity (Fig. 1a and Fig. S5a). Contrasting with our result, Wang et al. (2015) reported that the higher archaeal diversity was found at the more xeric areas in drylands and Angel et al. (2010) believed that archaeal diversity was not constrained by precipitation. Those contradictory findings might be attributed to the generalized 16S primer with only 0.8% of detected sequences could be affiliated to archaea and terminal restriction length polymorphism (TRFLP) technique adopted in their study, respectively. These methods are characterized by detection limit, low resolution and precision, thus may be expected to strongly influence the emerging diversity patterns (Schütte et al., 2008) and insufficient to cover the complexity of the intrinsic community (Kröber et al., 2009). Obviously, archaeal communities were more satisfactorily elucidated by performing high-throughput sequencing using archaea-specific primer pair in our study (Fig. S4). Thus, we strongly emphasized the loss of archaeal diversity following increasing aridity and the necessity for incorporation of not only bacteria and fungi which have been well documented to experience increasing-aridity-driven biodiversity losses

Table 1
Relative importance of environmental factors and geographic distance contributing to the variations in archaeal community composition based on multiple regression on matrices (MRM) model.

	All samples ($R^2 = 0.2124$, $p = 0.001$)	
	b	*p*-Values
Environmental factors	0.033	<0.001
Geographic distance	4.197E−5	<0.001

b: the partial regression coefficient. *p*-Values: the significant level.

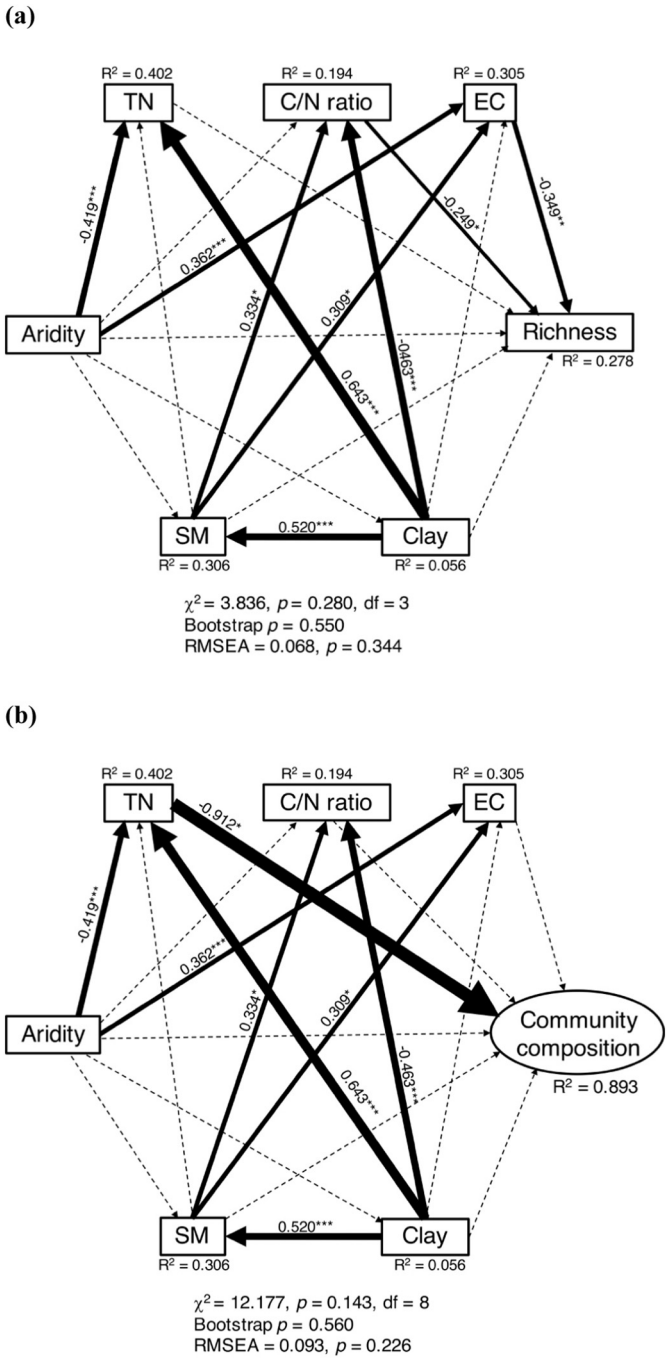

Fig. 4. Results of structural equation model for determining how aridity affected the (a) archaeal richness and (b) community composition. Continuous and dashed arrows represent significant and nonsignificant relationships, respectively. Numbers adjacent to arrows are standardized path coefficients that indicate the effect size of the relationship. The width of the arrows indicates the strength of the standardized path coefficient. The level of significance: $^{*}p \le 0.05$, $^{**}p \le 0.01$, and $^{***}p \le 0.001$.

(Maestre et al., 2012), but also archaea in assessing the impacts of climate change on ecosystems functioning.

Growing evidence suggests that many key drivers such as TN (Zhang et al., 2008), SOC (Moreno et al., 2009) and soil pH (Xia et al., 2016), for microbial communities exist threshold levels for triggering microbial responses that will result in concomitant and abrupt shifts in diversity or community composition (Baker and King, 2010). However, such thresholds have not been reported for climate factors such as precipitation and aridity. Our results demonstrated that 0.63 could be regarded as the critical value of aridity, before and after which the archaeal community composition changed pronouncedly (Fig. 2). Levels of annual precipitation at which bacterial community composition changed significantly was also reported by Yao et al. (2017). Given the microbial sensitivity to climate change (Liang et al., 2015), there might be a potential ecological threshold of climate factors for microbial structural responses to occur. This deserves particular attention in future research considering the important role of microbes in driving biogeochemical cycles.

4.2. The predominant role of niche-based processes in shaping the archaeal aridity-related pattern

The presence of distance-decay relation in this study suggested that variations in archaeal community composition along the aridity gradient could be, at least in part, explained by geographic distance (Fig. 3). The MRM model further demonstrated that niched-based processes dominated overwhelmingly in our study (Table 1). It is likely that drylands undergo sever nutrient depletion along with scarce resource availability (Delgado-Baquerizo et al., 2013a) as well as limited water availability (Nielsen and Ball, 2015), which thus may enhance the niche-based processes, such as environmental filtering, resources competition between species (Dumbrell et al., 2010), to select species with strong competitive and adaptive ability (Goberna et al., 2014). This is consistent with many previous studies which have observed greater determinism in extreme or limited resource environments (Stegen et al., 2012; Wang et al., 2017). Indeed, we found that aridity as a strong ecological filter excluded archaeal species that could not tolerate such environmental changes and kept most fit or best-adapted species from the native species pool (Fig. 5). At the phylum level, for example, increasing aridity promoted the dominance of archaeal major phylum *Euryarchaeota* (Fig. 2b and Table S3), which has been proved to be less sensitive to environmental pressures and more abundant in extreme environments (Cao et al., 2012; Takai et al., 2001). Additionally, based on indicator species analysis, we found that drier regions were more characterized by unclassified archaea compared with less dry regions (Fig. 5 and Table S4). This implies that evolutionary adaption through genetic change (Gubry-Rangin et al., 2011) or horizontal gene transfer (Lozupone and Knight, 2007) may occur in archaeal communities to survive and persist under increasing aridity-induced selective pressures. Since nutrient depletion and drought stress are accelerated with increasing aridity (Delgado-Baquerizo et al., 2013a; Huang et al., 2016), it seems that the relative influence of niche-based processes may increase as responses.

4.3. Indirect impacts of increasing aridity on archaeal communities

Soil EC provides an estimate of soil salinity (Bainard et al., 2014; Scudiero et al., 2016), which is sensitive to climate change (Neilson et al., 2017). It is reported that soil salinization accompanied with enhanced soil salinity is common in drylands (Luo et al., 2016; Thomas and Middleton, 1993). In this study, we also found that increasing aridity resulted in increased soil EC, which in turn diminished archaeal richness (Fig. 4a). This negative association is in line with previous studies form aquatic systems and soils (Bowman et al., 2000; Hollister et al., 2010) and suggests that indirect impacts of increasing aridity on archaeal diversity can be mediated by soil salinization in drylands.

Nitrogen as an essential nutrient element is, after water, the secondary important limited resources in drylands (Cookson et al., 2006; Wang et al., 2014). In this study, we found that TN displayed a negative correlation with aridity (Fig. 4), which is likely due to the higher soil erosion and the lower plant cover with increasing aridity in drylands (Delgado-Baquerizo et al., 2013a; Delgado-Baquerizo et al., 2013b). Structural changes in soil archaea were found to be closely related to those N-losses (Fig. 4b). A possible reason is that soil archaeal communities are sensitive to nitrogen concentration (Cao et al., 2012; Yao et al., 2014), and some archaeal populations such as AOA have specific nitrogen

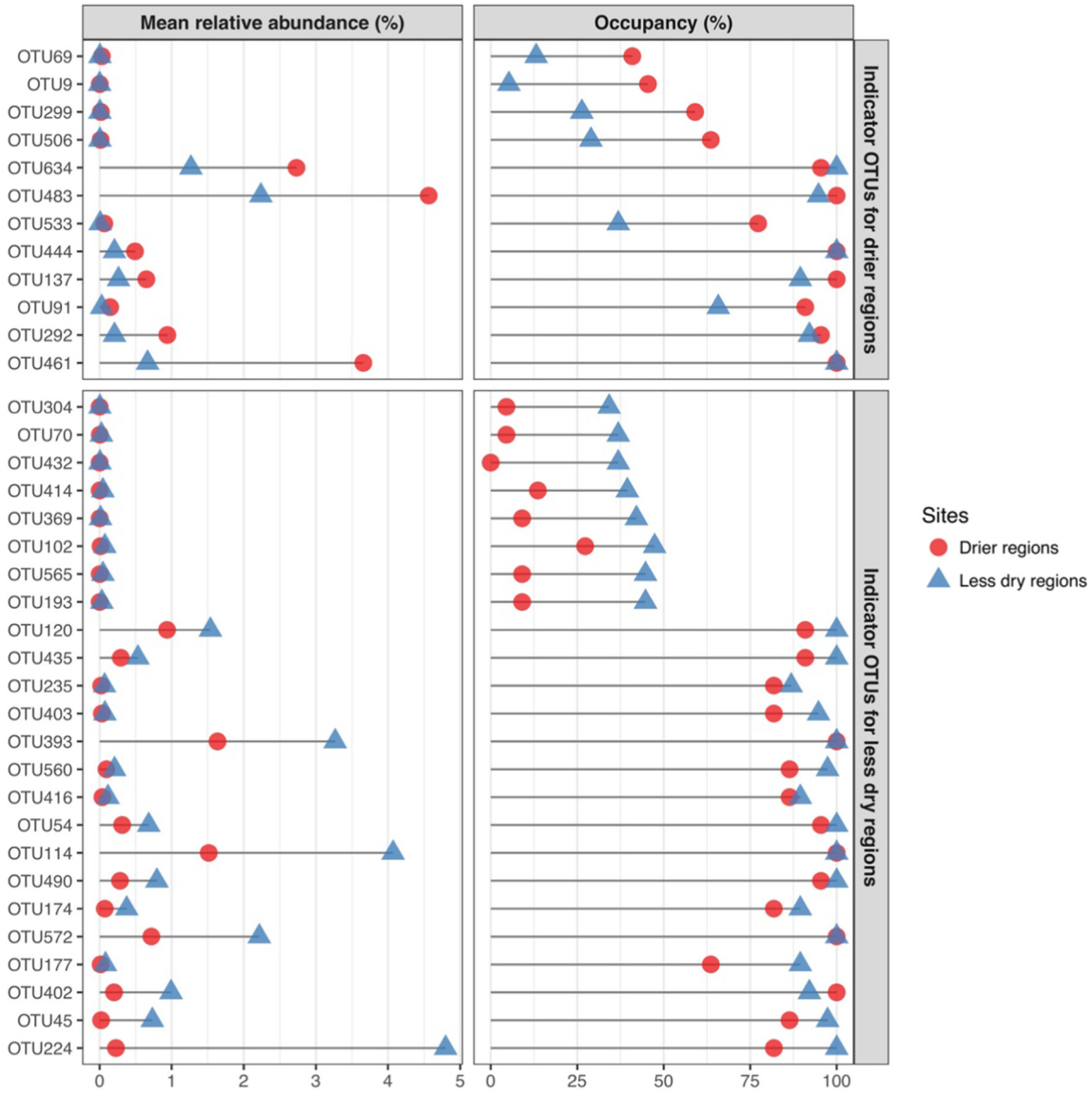

Fig. 5. The respective mean relative abundance (left panel) and sites occupancy (right panel) of indicator OTUs found in drier regions (top panel) and indicator OTUs found in less regions (bottom panel). Red circles represent sample sites in drier regions, while blue triangles represent sites in less dry regions.

conditions for optimal growth (Di et al., 2010). Evidence is increasing that many soil processes and functions such as gaseous decomposition, nutrient cycling and plant production are strongly driven by microbial community composition (Fierer et al., 2007; Peter et al., 2011; Trivedi et al., 2013). For example, Liu et al. (2018) believed that microbial community composition played a unique role in explaining the variation in soil respiration, which cannot be replaced by other key drivers for respiration. In this case, previous studies with focus on increasing-aridity-driven microbial diversity losses (Maestre et al., 2012) might be insufficient to predict the potential consequences of increasing aridity on terrestrial ecosystems. The incorporation of structural responses might be more effective for doing so.

Although archaeal diversity and community composition were directly influenced by different soil properties, our results collectively illustrated that indirect impacts of increasing aridity on archaeal communities were mediated by joint changes in soil niches. Due to their niche preferences, soil niches have been widely reported to play an important role in structuring archaeal communities (Bates et al., 2011; Chaban et al., 2006; Gubry-Rangin et al., 2011; Walsh et al., 2005). For example, AOA prefers to occupy soil niches with low water and nutrient availability (Adair and Schwartz, 2008; Valentine, 2007). Increasing aridity may promote shifts in soil niches via nutrient depletion, soil salinization and N-losses as discussed above, which thus can dramatically alter archaeal communities as we found here. Because archaea occupies a far more restricted ecological niche in soils than bacteria (Bates et al., 2011), it seems that niches mediating bacterial responses to increasing aridity might be independent from those of archaeal, highlighting the importance of paying more attention to archaea.

In conclusion, this study has provided insights into the role of increasing aridity expected with ongoing climate change as a force in structuring soil archaea in semi-arid regions in Inner Mongolia, China. Increasing aridity directly resulted in soil salinization and N-losses, which induced selective pressure and thus were paralleled by reductions in archaeal richness as well as dramatic alterations in community composition. These results demonstrate that soil niches as modulators of archaeal responses to increasing aridity are of paramount importance in predicting the alterations in archaeal communities under future climate scenarios. In addition, given the predominant role of archaea in nitrogen cycles in drylands, our results may help in understanding the

increasing aridity-induced imbalance between nutrient cycles reported by previous studies (Delgado-Baquerizo et al., 2013a; Jiao et al., 2016) and in assessing the systematic ecological responses to climate change.

Conflict of interest

This work has no actual or potential conflict of interest including any financial, personal or other relationships with other people or organizations.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.07.305.

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